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Incubating females use dynamic risk assessment to evaluate the risk posed by different predators

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Uncertainty poses a substantial problem for animals, making it is essential for individuals to anticipate changes in their environment to select suitable behavioral strategies. In nest-building species where parents care for dependent young, predation is a major cause of reproductive failure. However, because parents generally have inadequate information about nest predation risks, attaining information about predation hazards increases their likelihood of making informed, optimal decisions. Risk assessment should therefore be widespread, particularly in incubating parents of species that breed in cavities or closed nests, which have limited information about predator presence. This study experimentally investigated the dynamic risk assessment in incubating female brown thornbill (*Acanthiza pusilla*), a long-lived Australian passerine, which builds closed dome nests in dense vegetation. When the females were exposed to the calls of a nest predator, a predator of adults, and a nonpredatory species, they reacted most strongly to the predator of adults' calls, by looking out of the nest for longest. Females significantly increased their level of alertness on hearing calls of both predator species and maintained their higher level of alertness after the simulated predator presence ended. Females in nests with a high degree of visual cover, and therefore a larger information deficit, reacted more strongly to predator calls than females in more open nests. Moreover, poorly concealed nests had a higher probability of being predated. These results show that incubating female thornbills use dynamic risk assessment and base their response on who is at risk and the degree of information deficit. *Key words*: female information deficit, life-history, nest concealment, parental investment, predation. *[Behav Ecol]*

INTRODUCTION

Uncertainty poses a substantial problem for animals, so it is essential for individuals to anticipate changes in their environment in order to select suitable behavioral strategies (Dall et al. 2005). The better informed an individual is, the better it can respond and adjust to changes in its environment (Dall et al. 2005; Schmidt et al. 2010). However, animals generally have inadequate information on current risks (Bouskila and Blumstein 1992). A key variable inherently linked to uncertainty is the risk of predation, which directly affects an individual's fitness prospects. In nest-building species where parents care for dependent young, predation is a major cause of reproductive failure (Ricklefs 1969; Roff 1992). Thus, mechanisms for obtaining information and accurately assessing nest predation risk should be widespread as they will increase the probability of breeding individuals responding adaptively to risks, with positive repercussions for their survival and that of their offspring (Bouskila and Blumstein 1992; Schmidt et al. 2010).

Breeding birds face different predation risks during incubation as compared with other stages of the breeding cycle (Martin et al. 2000), and individuals should respond to these risks appropriately (Martin and Briskie 2009). For example, parents can react to variations in predation pressure and minimize movements to and from the nest, or choose better concealed nest sites (Ghalambor and Martin 2001; Eggers et al. 2006). During incubation, however, leaving the nest can be dangerous as parents may not be fully aware of nearby predators. This information deficit is particularly pronounced in species that build closed dome nests or breed in cavities (Collias 1997), as these birds have very limited information regarding the presence of predators and other threats in the surroundings. As a consequence, females of cavity nesting species have an increased mortality rate during reproduction (Lundberg and Alatalo 1992; Moorhouse et al. 2003; Donald 2007; Low et al. 2010), and it can be assumed that this is also the case for females of closed nest species. Thus, females of closed nest species are likely have evolved behavioral adaptations that reduce their information deficit and risk of being predated, although this remains unstudied (Lima 2009; Martin and Briskie 2009).

In this study, we experimentally investigated dynamic risk assessment by incubating female brown thornbill (*Acanthiza pusilla*), a small (7–9 g) yet long-lived passerine endemic to the forests of south-eastern Australia. Thornbills belong to the Corvida (Australian passerines) whose life-histories are characterized by small clutch size, a long breeding season with multiple nesting attempts, an extended period of postfledging care, and high juvenile and adult survival (Higgins and Peter 2002).

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The clutch size is 3±1 eggs, the incubation period is about 18 days, and nestlings remain in the nest for about 16 days (Green and Cockburn 1999; Higgins and Peter 2002). Female brown thornbills build a closed dome nest, typically in dense vegetation, and incubate the eggs without assistance from the male, which contributes to territory defense and the rearing of nestlings and fledglings (Green and Cockburn 1999).

We exposed incubating female brown thornbills to the calls of different predators, one posing a particular threat to eggs and nestlings (gray currawong *Strepera versicolor*) and one posing only a risk to the female (collared sparrowhawk *Accipiter cirrhocephalus*). We based our hypotheses regarding the response of incubating females on the life-history theory predictions for long-lived species (Williams 1966; Roff 1992). In that respect, species with a long lifespan and small clutch size have been shown to expose themselves to lower risks when defending current broods in order to protect investment in future broods (Ghalambor and Martin 2000, 2001). Particularly, we aimed at testing the following three hypotheses: 1) The risk assessment of females should differ for different risks, with females reacting more strongly to the predator of adults when minimizing the risk to themselves, and more strongly to the nest predator when minimizing the risk for their eggs; 2) Nest concealment should alter the response of females to predators, with females in better concealed nests having a greater information deficit regarding their surroundings. This could lead to females reacting more strongly (i.e. looking out of the nest) to a predator of adults, or to react less intensely (i.e. not looking out of the nest), as they are unlikely to be detected while on the nest. Nest concealment should only have a weak influence on the reaction of females to the nest predator, as they can escape the nest fast enough to evade this predator; 3) Breeding success could be affected by nest concealment and by female risk assessment. Nests may suffer higher predation because the nest location is disclosed to predators due to poor nest concealment, or by the female's responses to perceived threats.

MATERIALS AND METHODS

The field study was carried out at Trevallyn Nature Recreation Area (41°26'S, 147°05'E) close to Launceston, Tasmania, Australia. The vegetation in this study area consists of native woodland with mainly eucalypt and wattle stands, and an understory of large tussock grasses and bracken ferns. Between early October 2010 and early January 2011, we located brown thornbill nests and individually color-ringed birds in 75 breeding pairs. Brown thornbills re-nest after nest failure and may raise two broods per breeding season if the first nesting attempt is successful (Green and Cockburn 1999). Of the 85 nests we monitored, 61 were found during the building, laying, or egg stage. This facilitated our planned experiments during the incubation period. However, many nests were predated before the experiment ($N = 28$; overall nest predation rate 51%, during incubation 20%). In other cases, the incubating female was impossible to film (nest high up in tree; $N = 6$), or the female did not tolerate the camouflaged camera in the vicinity of the nest ($N = 4$). Thus, we could use a total of 23 nests in this experiment, and 83% of the individuals of these breeding pairs were ringed. All experiments, handling of birds and blood sampling, were carried out under the license of the University of Tasmania Animal Ethics Committee (license number A00110979).

Predator exposure experiment

We exposed 23 incubating females to the territorial calls of two different diurnal avian predators, a predator of adult birds (collared sparrowhawk; 125 g) and a brood predator (gray currawong; 350 g), which are known to prey on adult brown thornbills or their nest contents (Marchant and Higgins 1993; Higgins et al. 2006). Collared sparrowhawks are aerial ambush predators that hunt small birds and are thus a danger to adult brown thornbills (Marchant and Higgins 1993). Gray currawongs are omnivores that hunt by sight and sound within trees and on the ground and prey on both eggs and nestlings (Higgins et al. 2006). As a control, we presented the calls of an insectivorous passerine (dusky woodswallow *Artamus cyanopterus*; 35 g), which poses no predation threat to adults, eggs, or nestlings of brown thornbill (Higgins et al. 2006). All three of these species occur naturally at the study site.

The experiments were carried out during the second half of the incubation period because females were more sensitive to a camouflaged camera near the nest during early incubation. For each experiment, we positioned a digital video camera camouflaged with tree bark approximately 2–3 m from the nest and filmed the nest entrance to get a clear view of the female's behavior when on the nest. We set up a pair of speakers with built-in amplifiers (2 Watt output) connected to an MP3 player at about 8 m distance from the nest. The speakers were positioned so that the female could not see them or the experimenter when sitting on the nest. We started the camera, waited for the female to return to the nest and first filmed her behavior during one on-nest interval (i.e. amount of time the female spends on the nest incubating between foraging bouts) without treatment. The experimenter sat at least 10 m away from the nest, as the focal breeding pair proved not to be disturbed by human presence at this distance. Once the female had returned to the nest after a period of foraging, the experimenter started the playback that consisted of 10 min of silence followed by 5 min of calls (15–20 s of calls interspersed with 30 s of silence) by one of the predator species or the control species. For each experiment, we used unique call sequences to avoid the possibility of pseudoreplication. The same set-up was repeated in the subsequent on-nest incubation intervals for the two remaining types of calls. The interval between exposures was determined by the female's off-nest period (mean ± standard error [SE] = 30.7±2.9 min). In three cases, we were unable to finish an entire experimental block on the same day and returned to the nest on the next day to finish the experiment. The treatment order for the presentation of calls was randomized.

We analyzed the response of females to the different calls by examining the video recordings. Although females showed different behaviors while on the nest, preliminary analyses showed that the strongest behavioral change was in alert behavior. Because alert behavior is the most relevant behavior in antipredator vigilance, we only considered this variable in the analyses. For the statistical analyses, we manually extracted the following behavior variables and their duration (measured in seconds) from the video recordings:

1. Immediate response: Behavioral reaction shown by the female after start of the playback calls, which consisted of one of three mutually exclusive responses: head out, look up, or no noticeable reaction. Thus, females responded with vigilance to the calls (head out, look up) or not (no noticeable reaction) (see Results for more details).
2. Duration of immediate response: Time over which the female showed the immediate response.
3. Duration of alert behavior: Proportion of time over which the female showed alert behavior during the 5 min of exposure to calls and the 10 min before and after. Alert behavior comprised a tense body posture with the feathers

drawn close to the body, staring outside or sticking the head/half the body out of the nest entrance, turning the head to scan the environment.

The duration of alert behavior by the female was measured during the 5 min the calls were playing, as well as during the 10 min before and after. During the first on-nest interval with no experimental treatment, we measured the baseline duration of alert behavior during 5 min in the same way as during the experimental treatment. Because the duration of alert behavior was measured for a 10-min interval before and after the exposure to the calls and a 5-min interval during the calls, we standardized this variable to the mean number of seconds per minute for the statistical analyses. On five occasions, the immediate response could not be determined due to technical problems with the cameras.

Nest concealment

We measured nest concealment in the immediate surroundings of the nest to assess the effect of information deficit for the incubating female and the visibility of the nest to predators on her behavior during the predator exposure treatments. Nest concealment was taken as a standardized measure by an observer from 1 m distance at nest height and measured as the amount of vegetation by which the nest was covered as follows: The area directly around the nest (20 cm) was first divided into four quadrants that were projected onto the front of the nest, with the midpoint in the center of the nest (illustrated in Figure 1 in electronic appendix). Then, based on how many of the quadrants were covered by vegetation, nest concealment was classified as: Nest is fully concealed by vegetation ($N = 6$ nests), around three-fourth of the nest is concealed ($N = 4$), around half of the nest is concealed ($N = 7$), and nearly the entire nest is visible with two-third or less of the nest being concealed ($N = 6$).

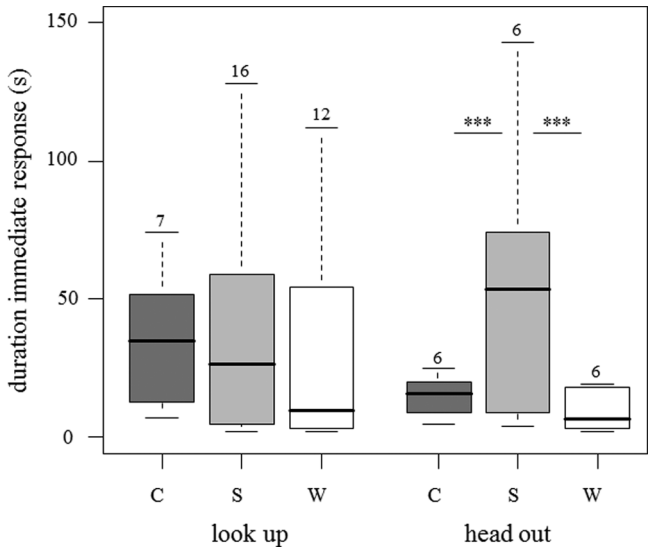

Figure 1
Duration (s) of the mutually exclusive immediate response behaviors head out and look up females showed on exposure to the calls of a nest predator (currawong = C), a predator of adults (sparrowhawk = S), and a nonpredatory species (woodswallow = W). Numbers over boxes show sample size ($N = 35$ look up, $N = 18$ head out). Statistically significant differences denoted by ***$P < 0.0001$. Information shown in boxplot: thick black line = median, lower/upper box borders = first/third quartile, whiskers = min/max data values.

Statistical analysis

We used general linear mixed models (GLMMs) with Satterthwaite degree of freedom estimation in SAS 9.2 (Glimmix and Mixed module; SAS Institute, Cary, NC) to analyze the data. In all models, we initially added all variables and interactions. However, including a certain interaction (call type × nest concealment) resulted in some models not converging due to sample size limitations and had to be removed. All mixed models had female identity fitted as a random effect to control for exposing the same bird to all three call types and were corrected for overdispersion where necessary. The effect of the different variables on female behavior was clarified with the help of least squares means (also called adjusted means). We first investigated whether the different calls affected the female's behavior compared with her baseline reaction by 1) testing the effect of call type (no calls compared with treatment calls), nest concealment, and the interaction between call type and nest concealment on the duration of alert behavior. In the subsequent analyses, we 2) tested the effect of call type, nest concealment, and the interaction between call type and nest concealment on the duration of the immediate response. We 3) tested which call type provoked the strongest change in the duration of alert behavior of the incubating female, both during the 5 min she was exposed to the call sequences and during the 10 min thereafter, compared with her behavior in the 10 min prior to exposure. Because the observations for a given nest and call treatment were assumed to be correlated, we used GLMMs with a compound symmetric covariance structure. As fixed effects, we included call type, exposure period (before, during, after the calls), nest concealment, and the interaction between exposure period and call type. Moreover, we 4) investigated whether brood survival was affected by the duration of alert behavior, the type of immediate reaction, and nest concealment using a binomial GLMM (with 0 = predated, 1 = successful; successful nests were classified as those fledging young).

RESULTS

Exposure to the playback calls had a strong effect on the behavior of incubating female thornbills, significantly increasing the time they were alert compared with their baseline behavior ($F_{3,56.7} = 13.6$, $P \leq 0.0001$). The calls of the predatory species had a particularly strong effect in this regard (for further details see Figure 2 in electronic appendix). Immediately after the start of the call sequences, incubating females showed three mutually exclusive behaviors: 1) they continued with their previous behavior, showing no noticeable reaction to the calls ($N = 7$), 2) they looked up with the head, the eye fixed on the nest entrance (hereafter referred to as "look up" $N = 35$), or 3) they stuck the head out of the nest entrance and scanned the surroundings (hereafter referred to as "head out" $N = 18$) (Figure 1).

Our key findings were that female thornbills reacted for longest, with the strongest immediate response (head out), to the calls of the predator of adult birds, the sparrowhawk (least square [LS] means ± SE: sparrowhawk 68.3 ± 3 s vs. currawong 16.4 ± 3 s, $P < 0.0001$; sparrowhawk 68.3 ± 3 s vs. woodswallow 9.6 ± 3 s, $P < 0.0001$) (Table 1, Figure 1). Females in fully concealed nests reacted longest with the response head out to the calls of the predator of adults (Table 1, Figure 3). The type of call played and nest concealment did not affect the immediate response look up (call type $F_{2,35} = 0.4$, $P = 0.7$; nest concealment $F_{3,35} = 0.9$, $P = 0.4$; call type × nest concealment $F_{5,35} = 0.4$, $P = 0.8$).

The duration of alert behavior by incubating females was significantly influenced by exposure period, call type, and

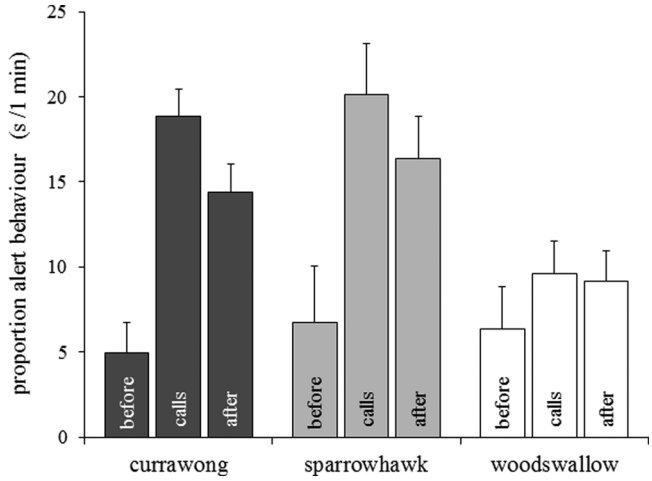

Figure 2
Change in the proportion of alert behavior (s/1 min, mean ± SE) shown by incubating females in the 10 min before and after the calls and in the 5 min during the calls. Duration of alert behavior standardized to the average number of seconds per minute.

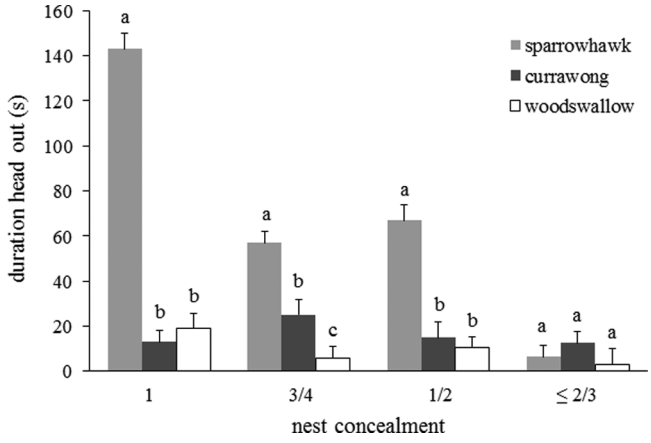

Figure 3
Duration (s) of the immediate response head out by predator type in relation to nest concealment. Different letters above the bars indicate statistically significant differences within each nest concealment category.

the interaction between exposure period and call type, but not nest concealment (Table 2, Figure 2). Incubating female thornbills adjusted the duration of alert behavior during the exposure periods (before, during, after the playback) depending on call type (Table 2, Figure 2). Compared with before the calls, females significantly increased their alertness during and after the calls on hearing a predator of adult birds or a nest predator close to the nest (LS mean differences for currawong: before vs. calls $t_{102} = -4.6$, $P < 0.0001$, before vs. after $t_{102} = 3.1$, $P = 0.003$; calls vs. after $t_{99.2} = -1.5$, $P = 0.1$. LS mean differences for sparrowhawk: before vs. calls $t_{100} = -5.8$, $P \leq 0.0001$, before vs. after $t_{100} = 4.2$, $P \leq 0.0001$, calls vs. after $t_{99.2} = -1.6$, $P = 0.1$). However, they showed no change when exposed to the calls of the control species (LS mean differences for woodswallow: before vs. calls $t_{99.2} = -1.2$, $P = 0.2$; before vs. after $t_{99.2} = 1.1$, $P = 0.3$, calls vs. after $t_{99.2} = -0.2$, $P = 0.9$) (Figure 2).

Brood survival was influenced by both nest concealment and female alert behavior. Less concealed nests had a higher risk of being predated than nests with a higher degree of concealment ($F_{3,99.2} = 2.7$, $P = 0.04$) (Figure 4), whereas the type of immediate response shown by incubating females did not affect brood survival ($F_{1,100} = 0.9$, $P = 0.3$). The duration of alert behavior showed a trend for increasing brood survival with higher female alertness, although differences were nonsignificant ($F_{1,100} = 3.2$, $P = 0.07$).

Table 1
GLMM of the effect of call type and nest concealment on the duration of the immediate response head out

Effect	n.d.f.	d.d.f.	*F* value	*P* value
Call type	2	18	112.8	<0.0001
Nest concealment	3	18	35.5	<0.0001
Call type × Nest concealment	6	18	27.9	<0.0001

Female identity was entered as random variable.
d.d.f. = denominator degree of freedom (estimated by the Satterthwaite method), n.d.f. = nominator degree of freedom.

Table 2
GLMM of the effect of call type, exposure period, and nest concealment on alert behavior before, during, and after call exposure

Effect	n.d.f.	d.d.f.	*F* value	*P* value
Call type	2	31.7	3.7	0.03
Exposure period (before, calls, after)	2	100	23.4	<0.0001
Nest concealment	3	14.4	0.2	0.89
Call type × Exposure period	4	100	2.8	0.02

Female identity was entered as random variable.
d.d.f. = denominator degree of freedom (estimated by the Satterthwaite method), n.d.f. = nominator degree of freedom.

DISCUSSION

Our results reveal that incubating female thornbills use dynamic risk assessment on hearing the calls of different predators. The immediate response of females was strongest on hearing the predator of adults, especially in fully concealed nests where females have a larger information deficit than females in less concealed nests (Figure 1, Table 1). Although individual females reacted differently to the calls of the predators and the control, the length of the immediate response was predator-specific and longest for the predator of adults. Moreover, higher female alertness tended to be associated with a greater brood survival probability, indicating that individual differences in risk assessment could be linked to breeding success. This suggests that incubating females simultaneously take several factors into account when assessing a risky situation, as discussed in detail below.

Gathering information is central for decision making and adaptive behavior by individuals (Dall et al. 2005). Previous studies on information acquisition and risk assessment by breeding individuals have mainly focused on breeding site selection and the benefits gained by using conspecific or heterospecific cues (Doligez et al. 2002; Emmering and Schmidt 2011). However, to our knowledge, this study is one of the first to examine risk assessment mechanisms to avoid predation

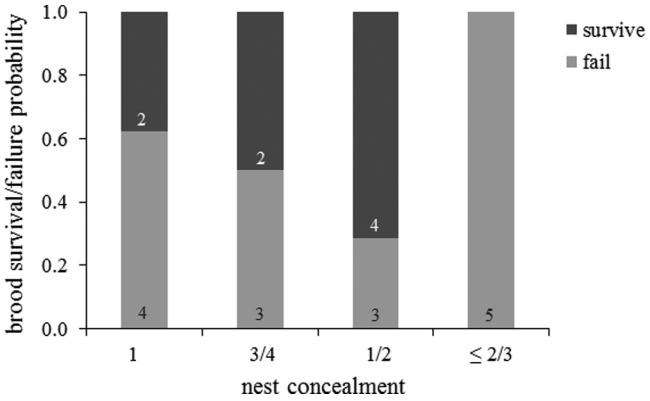

Figure 4
Influence of nest concealment on the probability of broods surviving or being predated. Numbers in the bars indicate sample size.

after nest site selection. Although breeding birds use acoustic or olfactory cues to select safer nesting sites (Mönkkönen et al. 2009; Emmering and Schmidt 2011), nest predation remains a potential risk, and especially during incubation, it can affect both brood and adult survival (Miller et al. 2007). Our results show that incubating female thornbills use dynamic risk assessment on hearing predator calls close to their nest. Although females reacted most strongly and longest to the predator of adults in terms of their immediate response, the calls of a nonpredatory species also elicited a risk assessment reaction in certain individuals. This finding goes along with the theoretical predictions of predation risk assessment, as overestimating a potential danger will increase the female's information level and allow her to minimize her mortality risks (Bouskila and Blumstein 1992). Further confirmation is provided by the fact that females maintained a high level of alertness after exposure to the predator calls. This issue has previously mainly been investigated in the foraging context, where individuals with incomplete information about a predator are more vigilant and resume their previous behavior later (Lima 1987; van der Veen 2002). For incubating individuals of closed nest species, which can be trapped by a predator in the nest (Collias 1997), continued alertness after danger may be important to gain vital escape time.

The risk of being detected by a predator and the chance of detecting an approaching predator are affected by large- and small-scale habitat structure and influence the level of antipredator investment (Griesser and Nystrand 2009). A high degree of cover in the breeding territory and around the nest can pose a trade-off for breeders, as it may not only provide protection from visually hunting predators but also provide more hiding places for predators and thus become a disadvantage for incubating females (Albrecht and Klvana 2004; Eggers et al. 2006; Cresswell et al. 2010). Better concealment of the nest can reduce the distance at which females can detect approaching nest predators, hinder their ability to correctly locate approaching predators, or even prevent them from detecting approaching predators altogether (Eggers et al. 2008; Magana et al. 2010). All of this can increase female mortality (Miller et al. 2007; Öst and Steele 2010). Although breeding in cavities and closed nests has been shown to reduce nest predation risk (Wesolowski and Tomialojc 2005; Auer et al. 2007; Brawn et al. 2011), females of such species suffer from a higher mortality rate during incubation than females of open-nesting bird species (Moorhouse et al. 2003; Donald 2007; Low et al. 2010). This trade-off between nest concealment and environmental information is confirmed by our finding that incubating female thornbills in fully concealed nests reacted most strongly to calls by the predator of adults, whereas females in less well-concealed nests also significantly increased their level of alertness when hearing the calls of a brood predator. Incubating females in closed nests generally face a higher information deficit through the structure of the nest itself, particularly when nests are located in dense vegetation. Females thus compensate for this information deficit by behavioral risk assessment mechanisms such as increasing the intensity with which they scan the nest surroundings (i.e. immediate response head out and look up).

Risk assessment forms the basis for making informed decisions and thus influences parental investment trade-offs under the threat of predation. This study highlights the trade-off between having a well-concealed nest and having a good view of the surroundings (Götmark et al. 1995). Dense vegetation around the nest can influence incubating females in two nonmutually exclusive ways. First, poorly concealed nests most likely are more easily detected by predators, as they faced a higher probability of being predated. Second, females breeding in well-concealed nests have to engage in more risk assessment to scan the surroundings. These females, by being more alert and assessing the risk more frequently, might respond more appropriately to predation threats and thus increase the survival of their brood. Individual risk assessment behaviors may thus mirror life-history decisions (Ghalambor and Martin 2001), as greater vigilance most likely not only increases brood survival but also female survival. Moreover, there may exist between-individual variation in how females resolve parental investment trade-offs, which could reflect differences in female age or personality (Nagy and Holmes 2005; Wolf et al. 2007), or be influenced by previous predator encounters. However, this study did not allow us to pinpoint the underlying mechanism driving this variation.

To conclude, our results demonstrate that incubating females use dynamic risk assessment to make informed, adaptive decisions. Risk assessment is likely to be an important proximate mechanism that links parental investment decisions to life-history strategies both across (Ghalambor and Martin 2001) and within species (as shown in this study).

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